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Over the past three years a special eye-movement monitoring and visual display system has been used to investigate human acuity using computer-controlled psychophysical testing procedures. The system can accurately measure eye-movements of less than 1' of arc and with the same precision, control the movement of visual targets relative to an observer's retina.

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The theoretical reconstruction of the response profile of a visual target is complicated by the fact that under ordinary viewing conditions, even during fixation, the population of active elements in the visual pathway changes constantly. Using the special visual apparatus, it was possible to maintain a target on a fixed set of retinal receptors facilitating an orderly experimental analysis of visual response patterns.

The problem of how the human visual system detects oriented targets was examined using a mathematical model whose basic elements are spatial filters representing the receptive field response profiles of visual cortical neurons in the supragranular layers of Area 17. The population response profile proved an accurate predictor of visual sensitivity for foveal targets.

PREDICTIVE MODELS OF

HUMAN VISUAL PROCESSES IN AEROSYSTEMS

Final Report

By

RICHARD J. W. MANSFIELD

DEPARTMENT OF PSYCHOLOGY

HARVARD UNIVERSITY

CAMBRIDGE, MASS. 02138

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I. Introduction

A central problem in the study of vision is the deter-
mination of the cellular neural mechanisms underlying
behaviorally relevant functions. Unfortunately, no single
approach or technique has proved sufficient by itself to
unravel all the complexities involved and provide a complete
understanding of visual behavior. Precise assessment of
behavioral performance with well-defined tasks in the intact
animal can yield a quantitative description of visual
behavior but any inferences concerning causal neural mecha-
nisms must remain speculative since the central nervous
system of any species of interest is too complicated for a
unique mechanism to be identified. As Dean describes
in a discussion of the inferotemporal cortex elsewhere in
this book, the same limitation applies to behavioral studies
of lesioned animals. At the other end of the spectrum
of approaches, neuronal activity can be measured directly
at some level of the visual pathway by fracturing the
integrity of the central nervous system with anesthesia,
drugs or surgery,and with the application of techniques from the
armamentarium of modern neurobiology, specific cellular
mechanisms can often be identified. However, as several
chapters in this book emphasize, visual processing in the
central nervous system is distributive, that is to say there
are multiple visual systems, so that a particular candidate
mechanism may be irrelevant to the behavior of interest or
may operate differently in the intact animal. However,

converging evidence from different approaches to the study
of the visual system can offer an effective strategy.

The primate striate cortex provides a model system to
illustrate such a strategy. Considerable information has
accumulated concerning the anatomy and physiology of the
striate cortex and antecedent structures in the retino-
geniculo-cortical pathway. In contrast to the afferent
visual pathways of other species (see for example the afferent
pathways in the cat as illustrated in Fig. 1 in the chapter
by Berkley and Sprague) the striate cortex in Old World
anthropoids is the major if not exclusive recipient of fine-
grain visual information. For Old World anthropoids the
cross-species similarity assumption appears valid, so that
behavioral and neural data obtained for one species can be
assumed to hold for all others. To explain visual perfor-
mance in general, a reasonably complete if not exhaustive
knowledge of the central nervous system is required, but
for optimal performance such as that in a visual acuity task
we need only focus on the relevant mechanisms that provide
constraints on optimality. Strong evidence places the locus
of such constraints in the striate cortex, and the quantifi-
cation of striate receptive fields and visual performance on
acuity tasks makes possible the development of a computational
theory relating causal neural mechanisms to behavior. In
this chapter a combined approach of neural and behavioral
analyses and mathematical synthesis is applied to the role
of the striate cortex in visual acuity. First those critical
features of the primate visual system that are pertinent to the
discussion are reviewed.

II. Primate Anatomy and Physiology

Existing Old World anthropoids which includes a range of
species from monkey (e. g. macaca mulatta) to man (e. g. homo
sapiens) exhibit a number of special evolutionary adaptations in
their visual systems. These species most probably having evolved
from nocturnal, solitary visual predators (Cartmill, 1974;
Polyak, 1957) into diurnal, social frugivores or omnivores
possess frontally directed eyes with large degree of
binocular overlap of 150°, high central visual acuity (Blakemore,
1970), well developed trichromacy (DeValois and Jacobs, 1968)
and stereopsis to baffle natural camoflage and promote their
precise eye-hand coordination, excellent visuospatial memory
(Menzell, 1973) and acute perception of visual social cues
(Savage-Rumbaugh, Rumbaugh and Boysen, 1978). Subserving these
behavioral adaptations there are a number of neural adaptations
not all of which are known or understood at the present time.

A. Foveal specialization

The retina of Old World anthropoids and indeed of a number
of other primates possesses a specialization corresponding to
the center of visual fixation, the fovea. As in all vertebrate
retinas the photoreceptors are located at the inner margin of
the retina facing away from the light. However, in the primate
retina at the region corresponding to the center of gaze the
proximal neurons in the inner nuclear layer (amacrine and
ganglion cells) are displaced laterally forming the foveal
pit and allowing light more direct access to the transduction
elements. Reduction in light scattering is also achieved by
avoidance of the foveal region by the blood vessels on the

vitreal surface of the retina leaving intact only the choroidal

circulation. Associated with the ciliary stocks of the photo-

receptors in the fovea (cones) is the dense yellow pigment, the

macular pigment, which serves to absorb shortwave light and reduce

the chromatic abberation inherent in the simple lens system of the

eye. Flicker photometry measurements (Wooten, Thawley and Knoblauch,

1980) indicate that the macular pigment is densest in the center of

the fovea with its distribution dropping off sharply outside the

fovea in parallel with the cone distribution. Microspectrophotometric

measurements of cone outer segments have revealed a basis for tri-

chromatic color vision in the differing absorption spectra with

λ_{max} of 430nm, 535nm, 565nm (Marks, Dobell and MacNichol, 1964;

Wald and Brown, 1965; Bowmaker, Dartnall and Mollon, 1980)

described by a modified vitamin A_1 nomogram (Ebrey and Honig,

1977). Although the center of the fovea is rod-free the dense

packing of the cones distorts the outer segment into slender rod-

like shape (Dowling and Boycott, 1966) from their normal pyramidal

shape found in the periphery. Although rods and cones probably

do not differ significantly in intrinsic sensitivity (Fain and

Dowling, 1973) they do exhibit substantially different saturation

characteristics (Boynton and Whitten, 1970). The convergence

necessitated by the existence of 200 million photoreceptors

but only 1 million optic nerve fibers is not uniform but

graded across the retina with the central region receiving a

disproportionate share as reflected in the magnification

factor in the retinotopic map of the dorsal lateral geniculate

(Malpeli and Baker, 1975). In contrast to other vertebrate

species the retinal circuitry of Old World anthropoids is
simple containing relatively few classes of amacrine cells
and correspondingly the retinal ganglion cells fall into
relatively few classes. Following terminology developed in
the cat retina, ganglion cells have been classified into three
classes termed X, Y and when specified, W (DeMonasterio
and Gouras, 1975; Schiller and Malpeli, 1977; DeMonasterio,
1978a). X cells have small receptive fields, summate linearly
across these fields, frequently have a sustained response
to standing contrast and are found predominantly in the
foveal region. Y cells have large receptive fields, summate
nonlinearly across these fields, mainly exhibit a transient
response to standing contrast and are found predominantly in
the periphery. In quantitative terms the central fovea (1°)
yields 90% X cells and 10% Y cells, but in the near periphery
($11-20^{o}$) only 45-70% X cells and 30-50% Y cells (Schiller and
Malpeli, 1977; DeMonasterio, 1978a). W cells, clearly not a
homogeneous class, lack well defined center-surround organi-
zation, are distributed across the retina but mainly outside
the foveal region, and project directly to the superior
colliculus rather than through the geniculate with some
exceptions (Wiesel and Hubel, 1966; Dreher, Fukada and Rodieck,
1976; DeMonasterio, 1978b) providing in the primate (in
contrast to other mammals) a complete representation of only the
contralateral half of the visual field. The actual proportion
of the retinal ganglion cell distribution consisting of W cells
is difficult to estimate since the recording techniques tend

to sample from the larger or more responsive X and Y cells.
Rodieck (1979) estimates that possibly 50% of cat retinal
ganglion cells are W cells, so that in monkey the proportion
may be larger than the 10% encountered experimentally. The
retinal segregation into separate functional classes undoubtedly
has adaptive significance since it is retained at higher
levels in the visual system.

B.   Functional segregation in the dLGN

The axons of the retinal ganglion cells form the optic
nerve which decussates at the optic chiasm before reaching
its targets in the dorsal region of the lateral geniculate
of the thalmus and the superior colliculus in the brain stem.
Each hemi-retina has a geniculo-cortical target in a separate
hemisphere except for a 1° vertical strip along the midline
and a few ganglion cells around the rim of the fovea 'Stone,
Leicester and Sherman, 1973; Bunt, Minckler and Johanson, 1977).
The primate dLGN is a 6-layered structure receiving in
precise retinotopic register the inputs from the two
retinas and maintaining them in separate laminae with a
discrete functional organization as well (Schiller and Malpeli,
1978; Dreher, Fukada and Rodieck, 1976). The 4 parvocellular
layers receive X cell input and have cells with concentric
color-opponent receptive field organization (R+G- or G+R-);
the blue-selective on-cells are found predominantly in the
ventral pairs of parvocellular layers. The two magnocellular
layers receive Y cell input and have cells that are concentri-
cally organized but as might be expected have spectrally
broad band or achromatic receptive fields.

C. Cortical organization

In contrast to other mammalian species (e.g. see the chapter by Berkley and Sprague for a discussion of the multiple and parallel input pathways into the cortex of the cat) the dLGN of catarrhine monkeys, apes and man forms the major if not exclusive input into the cortex, and that entry is confined to the striate cortex (Area 17 of Brodman) as shown in Fig. 1.

Insert Fig. 1 about here

Moreover the functional segregation present in the geniculate is maintained though less strictly in this initial cortical stage. The axons of the X cells of the parvocellular layers terminate mainly in layer 4A and layer 4Cβ of this 6-layered koniocortical region (Hubel and Wiesel, 1972). The field of termination is the spiny stellate neurons which project to layer 3B and 5A as well as within 4C (Lund, 1973; Lund and Boothe, 1975). The axons of the Y cells emerging from the magnocellular layers project mainly to layer 4Cα (Hubel and Wiesel, 1972); however, they also bifurcate and terminate in the superior colliculus (Schiller, Maipeli and Schein, 1979). The field of termination is the spiny stellate neurons which contribute to laminae 4B and 5A but also distribute widely within 4Cα (Lund, 1973; Lund and Boothe, 1975). Both anatomical evidence based on Golgi staining (Lund and Boothe, 1975) and electrophysiological evidence based on selective anesthetization of a specific geniculate lamina (Schiller, Malpeli and Schein, 1979) suggest that the input from the parvocellular and magnocellular geniculate neurons remains largely segregated with X cells being the dominant

influence for cortical neurons with cell somas in the upper
or supragranular layers and Y cells being the major influence
for the infragranular layers. Such a distinction has a
definite functional significance since the efferent pro-
jections of the two regions are quite different.

Area 17 or V1 projects and receives reciprocal projec-
tions from both cortical and subcortical targets with the
cortical targets receiving efferents predominantly from the
supragranular layers and the subcortical targets receiving
efferents from the infragranular layers (Lund, Lund,
Hendrickson, Bunt and Fuchs, 1975).
The pyramidal cells in the upper regions of layer 6 project
back inhibitorily to the parvocellular layers of the dLGN
but the pyramidal cells in the lower portion of layer 6
project back to the magnocellular layers (Marocco, McClurkin
and Farooqui, 1979). The pyramidal cells in layer 5 project
retinotopically to both superior colliculus and pulvinar
but receive a reciprocal projection to layer 2 only from
pulvinar which also projects widely to the rest of the visual
field (Diamond, 1979). However, the projection from the
pulvinar to the more rostral regions of cortex does not
contribute to the spatial selectivity of the cells in these
regions (Gross and Mishkin, 1977). Both the pyramidal and
stellate cells in layer 4A which exhibit strong directional
selectivity(Dow, 1974) as well as the largest pyramidal cells
in the upper portion of layer 6 project to MT which in turn
sends a reciprocal projection to layers 4A and 6. This circuit

may contribute to visually guided movement rather than object
vision since MT sends a heavy projection to the pontine
nucleus which then relays the information to the cerebellum
(Glickstein, 1979). The pyramidal cells in the supragranular
layers project transcortically to V2 and V3 both ipsilaterally
and near the V1/V2 border contralaterally as well; these
regions reciprocate with a projection to layer 1 (Spatz and
Tigges, 1972; Wong-Riley, 1979). In addition there is a
recently discovered third cortical projection site in the most
caudal portion of the interparietal sulcus (see chapter by
Ungerleider and Mishkin for a review of the evidence for the
site). The cortico-cortical pathways from the supragranular
layers conveying the transformed input from the parvocellular
X cells are undoubtedly the critical ones for pattern vision.

     Since in primates but not other mammals V1 is the
dominant if not exclusive entry site of visual information
into the cortex, the supragranular layers of V1 as indicated
in Fig. 1 are the gateway to an arena of rich cortical inte-
gration. The terminal target regions in the visual projection
field have been implicated in different classes of visual
behavior: (1) MT could play a role in visually guided
movement (Glickstein, 1979); (2) Area TE of von Bonin and
Bailey on the inferior convexity of the temporal lobe appears
to mediate the acquisition of complex visual discriminations
(Gross and Mishkin, 1977; see chapter by Dean in this book);
(3) Area 8 in the frontal lobe serves as a second control
center for saccadic eye movements in addition to the superior

colliculus (Schiller, True and Conway, 1979); (4) Area 7
in the parietal lobe appears to direct visual attention to
objects in extrapersonal space (Lynch, Mountcastle, Talbot
and Yin, 1977; Mountcastle, 1978; see chapter by Ungerleider
and Mishkin in this book for evidence from lesion studies
implicating this region in object localization). However,
these more rostral regions of the visual system may be
irrelevant or at least redundant for certain basic pattern
detection tasks since all regions of the cerebral cortex
project to the basal ganglia, the major motor control system.
In particular, visual acuity is unimpaired by either infero-
temporal lesions (Cowey and Weiskrantz, 1967; Blake, Jarvis
and Mishkin, 1977; Weiskrantz, 1980) or by parietal lobe
ablation (see chapter by Ungerleider and Miskin in this book)
which suggests that some relatively simple detection mechanism
applied to the output of Area V1 may be sufficient for high
level performance in a visual acuity task. It is of interest
then to consider how visual information is processed in V1
and represented in the population profile of its efferents.

III.   Cortical Processing and Representation in V1

In order to analyze the contribution of V1 it is necessary
first to consider visual information that remains essentially
invariant so as to define more clearly the intrinsic processes.

A.   Invariants of retinal and geniculate origin

The receptive fields of individual neurons recorded in
the supragranular layers of striate cortex preserve invariant
or only slightly transformed several properties encoded in
more distal portions of the visual pathway. The minimum
discharge receptive fields are discrete with excitatory cores
only slightly greater in size than those of the dLGN (Schiller,
Finlay and Volman, 1976a) maintaining approximately the same
magnification factor as in the geniculate (Hubel and Wiesel,
1974) but with a somewhat less precise retinotopic organization.
Light- and dark-adaptation have their major locus of control
in the retina so that for example the inverse relation
between discharge latency and the luminance of the background
or target is determined up to an additive constant by retinal
and in the dark-adapted case more likely by photoreceptor
mechanisms (Mansfield, 1976b; Mansfield and Daugman, 1978).
Object brightness which appears to be encoded by relative
impulse density is established for isolated targets at the
retinal ganglion cell level in a relation that is initially

linear up to one log unit above the background level but
nonlinear at higher levels (Mansfield, 1976a,b; 1975). In
the dark-adapted case, simple reaction time and the latency
of cortical evoked potentials decrease as the inverse cube root
of target luminance approaching asymptotically different
but constant values. In the dark-adapted case, retinal
ganglion cells, lateral geniculate neurons and supragranular
striate cells (although only 10% of the population) increase
their average discharge rate as the cube root of target
luminance, a relation also found with numerical magnitude
estimates in psychophysical tasks. However, the brightness
or lightness of targets in more complex scenes is influenced
by large range spatial interactions (e. g. Land and McCann,
1971) which undoubtedly reflect central convergence. Such global
interactions of lightness may underlie object color perception
but local spectral and achromatic differences are present
more distally. The majority of neurons in the supragranular
layers of the foveal projection region maintain a differential
sensitivity to wavelength (Poggio, Baker, Mansfield,
Sillito and Gregg, 1975; Crawford, Fagan, Borchert, Heston
and Marc, 1979) but in the representations of the more
peripheral regions the proportion drops sharply relative to
that of the geniculate indicating some convergence. In
addition, the constant criterion thresholds of the monkey
spectrally broad band cells in both the foveal and parafoveal
projection regions reflect the same balanced input from the three

classes of cone photoreceptors exhibited by behavioral
measures of luminance threshold in the intact animal (Poggio
et al, 1975). On the other hand, four attributes of cortical
receptive fields represent intrinsic contributions of
striate cortex.

B.   Intrinsic cortical transformations

There are four major transformations carried out upon
the incoming visual information by the synaptic circuitry of
V1 and reflected in the discharge patterns of efferent
neurons: (1) binocular convergence; (2) spatial frequency
filtering; (3) pattern specific adaptation; (4) orientation
and direction selectivity. For each visual hemifield V1
represents the first site of binocular convergence. With
increasing distance from layer 4 the proportion of binocularly
driven neurons increases in a manner suggesting independence
of connectivity for orientation selectivity and ocular
dominance (Poggio, 1972). Although the degree of orientation
preference disparity, i. e. the amount to which the axis
of orientation differs in the two eyes is small in primates,
estimated to be 4° in the macaque monkey compared with 9°
in the cat (Mansfield, Ronner and Daugman, 1980), there is
also a binocular disparity in the retinal locus of receptive
fields that probably serves a role in local stereopsis.
Poggio and Fischer (1977) found that in the foveal striate
projection region where receptive fields were small the
majority of neurons were sensitive to location of stimuli
in depth with the maximum discharge or shift in discharge
occurring within $\pm\ 0.4^{\circ}$ of disparity but the total range

of binocular interaction could extend to more than $\pm 1^{\circ}$ of
disparity. A second transformation that takes place is
that the spatial frequency filtering present in the geniculate
neurons becomes sharper (Poggio, Doty and Talbot, 1977;
DeValois, Albrecht and Thorell, 1978). The third transformation
is the adaptation or habituation of neural discharges to
specific patterned stimuli (Mansfield, Ronner and Daugman,
1978) a feature not observed in the lateral geniculate
(DeValois et al, 1978; Wiesel and Hubel, 1966; Schiller and
Malpeli, 1978) but whose appearance at the cortical level
reflects the initiation of a temporal filtering mechanism
for visual salience and novelty. A fourth and major transfor-
mation is that instead of isotropic, concentrically organized
receptive fields such as those found in the dLGN the majority
of striate neurons in the supragranular layers exhibit an
orientation preference and are directionally selective
(Hubel and Wiesel, 1968; Poggio, 1972; Dow and Gouras, 1973;
Dow, 1974; Poggio et al, 1975; Schiller, Finlay and Volman,
1976a,b; Mansfield et al, 1980). From recent experiments
quantitative estimates can be made of the population response
characteristics in the efferent projection from V1.

C. Quantitative measurements of receptive field properties

In order to predict behavioral performance it is
necessary first to know in quantitative detail the excit-
ability profiles of the receptive fields of the efferent
neurons in the supragranular layer and secondly to understand
at least to a first approximation how the neural information is
utilized in a particualr behavioral task.

For the first problem the main obstacle is that of sample bias when recording from only a small proportion of neurons in the layers. One source of sample bias arises from the columnar organization for the attributes of orientation selectivity and ocular dominance (Hubel and Wiesel, 1963). The invariance of particular receptive field properties with cortical depth is a general principle of neocortical organtation (Mountcastle, 1957; Mountcastle, 1978) probably reflecting the conservation of genetic information required for synaptic organization of the cortex using modular subunits. From the experimenter's point of view, however, microelectrode penetrations normal or nearly normal to the pial surface encounter neurons whose receptive field properties are not independent; oblique penetrations encounter similar problems of statistical dependence when the attributes like orientation selectivity exhibit sequential regularity (Hubel and Wiesel, 1974). One strategy for obtaining statistical independence is to count as a sample only a single neuron's receptive field (e.g. the first neuron encountered that could be studied) in a given penetration and to separate penetrations by at least some fixed distance (e.g. at a separation of 500 microns the mean serial correlation coefficient for orientation preference has dropped to chance levels) (Mansfield, 1974; Mansfield et al, 1980). A second potential source of sample bias with microelectrode penetrations is that the neurons with large cell somas will be more heavily weighted since their action potentials will be more easily isolated (Humphrey and Corrie, 1978). However, since the

neurons of interest are the pyramidal cells in layers 2-3
rather than the stellate cells such a bias will aid in selecting
the population of interest. A third potential source of
bias is the stochastic nature of the neuronal discharge;
however, multiple and randomized stimulus presentation
can provide objective, stable measures (Stryker and Sherk,
1975; Schiller, Finlay and Volman, 1976a; Mansfield et al, 1980).
A fourth potential source of bias is that a particular choice
of measure for neuronal discharge may not be relevant for
further processing by the more rostral portions of the visual
system; however, integrated discharge (pulse number) for
brief stimulus presentations is a probable candidate code.

1) Excitability profiles

The majority of the receptive fields in the supra-
granular layers of primate V1 have discharge characteristics
resembling X cells in the geniculate but spatial character-
istics of complex cells, i.e. a single activating region
(Hubel and Wiesel, 1968; Poggio et al, 1975; Schiller et al,
1976a; Poggio et al, 1977; Mansfield et al, 1980). No receptive
field type, e.g. simple cells, is distinguishable on the
basis of receptive field size or breadth of orientation
tuning (Schiller et al, 1976; Mansfield et al, 1980). At
the descriptive level a central excitatory zone with flanking
silent cortical inhibition of cortical origin is a first
approximation.

2) Orientation tuning

As with orientation tuning curves in the cat when they
have been examined in quantitative detail (Henry, Dreher and

Bishop, 1974), a symmetric bell-shaped curve provides an **excellent**

fit to primate data as illustrated in Fig. 2 for a binocular cell.

Insert Fig. 2 about here

The shape of the orientation tuning curve does not change systemati-

cally with orientation preference or with retinal eccentricity at

least between the central foveal projection (0-2°) (Mansfield et al,

1980) and parafoveal region (3-6°) (Schiller et al, 1976b; Mansfield

et al, 1980) where it has been examined. However, as illustrated in

Fig. 3 the distribution of tuning bandwidths (half-width at half-height)

Insert Fig. 3 about here

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is broad but skewed toward the narrowly tuned neurons with a median

near 24°, a value that is consistent across electrophysiological

experiments (Schiller et al, 1976; Mansfield et al, 1980). One strik-

ing difference illustrated in Fig. 4 between foveal and parafoveal

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Insert Fig. 4 about here

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projection regions is that in the parafoveal projection region all

orientations are equally represented (Hubel and Wiesel, 1968; Finlay,

Schiller and Volman, 1976) but in the foveal projection region the

horizontally and vertically selective receptive fields are over-

represented (Mansfield, 1974; Mansfield and Ronner, 1978; Mansfield

et al, 1980). The orientation anisotropy is probably innate and is

not confined to primates (e.g. for the cat: Pettigrew, Nikara and

Bishop, 1968; Levanthal and Hirsch, 1977; Kennedy and Orban, 1979;

Orban and Vandenbussche, 1979).

3)   Size or spatial frequency tuning

The size of receptive fields in the supragranular layers changes
with two gradients. First the average size of receptive field
increases with retinal eccentricity (Hubel and Wiesel, 1974). Second,
the size of receptive field increases with distance from layer 4, the
main input layer. So that at each location in the retinotopic pro-
jection there is a distribution of receptive field sizes. One method
of quantifying the degree of size tuning of the cell is to measure
the response of the cell to grating targets. When displayed along
a log spatial frequency axis the response curves assume a shape that
is approximately 1 - 2 octaves wide at half-maximal response (Schiller,
Finlay and Volman, 1976c; Poggio et al, 1977) or at half-maximal
sensitivity for a constant criterion response (DeValois, Albrecht and
Thorell, 1978). The available samples of neurons from the supragranular
layers for which optimal spatial frequency has been measured are
relatively small but an approximation to the distribution is shown
in Fig. 5. An additional factor is the degree to which neurons with

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Insert Fig. 5 about here

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different optimal spatial frequencies respond at their optimal fre-
quency to contrast differences; however, there is essentially no
quantitative data that can be brought to bear on this question.

4)   Pattern-specific adaptation

A common observation is that neurons in the supragranular layers
are difficult to activate repeatedly and habituate easily (Wurtz,
1969). The decrement in response is exponential with time and
depends upon the cell's response, i.e. non-optimal stimulation does
not produce habituation (Mansfield, Simmons and Daugman, 1979). The

exponential time constants vary across cells and are smaller for
adaptation than for recovery in which case the average value is
on the order of 10 sec. Direct synaptic activation of the supra-
granular pyramidal cells produces habituation in vitro (Mansfield and
Simmons, 1979)that follows a similar time scale for recovery.

5)   Quantitative model of population response profile

        In order to develop a computational theory of the function
of the supragranular layers of V1 based on the population response
profile, we need to consider first the excitation profile of a
typical cortical receptive field in the supragranular layers; second,
the local and global distribution of receptive field parameters;
and finally a candidate algorithm for combining the neural output
from V1 to produce a response.

i)   Cortical receptive field excitation profile

        The experimental studies reviewed above indicate that the
cortical receptive fields in the supra-granular layers are
shape-invariant with changes in preferred orientation and
scale multiplicatively in the frequency domain. As a
simplified but instructive approach to the question of the
construction of a cortical receptive field, we can consider
how the receptive fields at successive levels in the primate
visual system are generated. For convenience, the on-center
retinal ganglion X cell will be used as an example. The
spatial domain weighting function describing the contributions
of the photoreceptor input to the cell can be reasonably well
approximated by a circularly symmetric Gaussian distribution,
the expected limiting distribution as the number of photo-

receptors becomes large assuming isotropic and globally random connec-

tivity. However, lateral inhibition is also contributed by the retinal

circuitry and can be represented by the simplest isotropic form of

spatial differentiation, the two-dimensional Laplacian operator, ∇^2,

defined as

$$\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} \tag{5.1}$$

or more simply as $\frac{\partial^2}{\partial r^2}$ for circularly symmetric spatial functions

in polar coordinates. The resulting excitation profile, E(r), for

the retinal ganglion cell is given by the equation

$$\nabla^2 G = ?(\frac{r^2}{a^4} - \frac{1}{a^2})e^{-(\frac{r}{a})^2} \tag{5.2}$$

respresenting central excitation with surround inhibition as depicted

in Fig. 6. The profile is essentially similar to the empirically

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Insert Fig. 6 about here

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derived difference of Gaussians used by Enroth-Cugell and Robson (1966)

to describe the structure of cat retinal ganglion cells. At the next

level in the parvocellular layers of the lateral geniculate, the

principal cells receive excitatory input from probably a very small

number of retinal ganglion cells of the same type (on-center). No

inhibition is directly transmitted but rather is supplied by inhibitor\

interneurons. The profiles would remain essentially isotropic and

unchanged in shape except for stronger inhibition since the lateral

inhibition is applied on the afferent side rather than on the efferent

side. At the cortical level the geniculate input is probably exclusively

excitatory and supragranular pyramidal cells probably receive direct

monosynaptic contact from very few geniculate axons. Inhibition is

supplied by di-synaptic or polysynaptic circuits. Since the intra-

cortical inhibition is polysynaptic, the inhibitory subfields are

larger than the excitatory central zone as well as being slightly

displaced. The inhibitory side lobes although silent could generate

orientation selectivity and the width of the excitatory central zone

could determine the optimal size or spatial frequency tuning for the

cell. A second operation of lateral inhibition is suggested by the

recurrent collaterals of pyramidal cells as are found elsewhere in

the neocortex (Marin-Padilla, 1969; 1970) and by the difficulty in

generating responses by electrical stimulation in the optic radiation

below the cortex. Antidromic action potentials would serve to silence

cellular activity by recurrent inhibition. Such pericolumnar inhibition

as Mountcastle (1978) has described it would by the sequential regularity

of the orientation columns be directed orthogonal to the preferred

orientation. Formally in terms of the simple theoretical receptive

field profile described by Equation 5.2, the Laplacian operator takes

the form ∇_x^2 if for convenient we let the y-axis be the axis of

preferred orientation. When the operator is applied the equation for

the receptive field profile becomes

$$\nabla_x^2 \nabla^2 G = \left[\frac{8r^4(\cos\theta)^2}{a^6} + r^2\left(\frac{8(\cos\theta)^2}{a^6} - \frac{16r^2}{a^4} - \frac{4}{a^6}\right) + \frac{8}{a^4} \right] e^{-\left(\frac{r}{a}\right)^2} \qquad (5.3)$$

The receptive field profile corresponding to Equation 5.3 is shown

in Fig. 6. The pericolumnar inhibition would have the effect of

sharpening orientation and frequency tuning.

ii) Local and global population parameters

        At a given point in the cortex a typical receptive field

can be described by an excitation profile such as that given by

Equation 5.3. Such a receptive field then acts as a local spatial

filter with a particular center frequency and frequency bandwidth and

preferred orientation and orientation bandwidth. Locally the center

frequency is distributed as illustrated in Fig. 5, and the frequency

bandwidths at half height are distributed in a small range between

1 and 2 octaves. Depending upon location the orientation preferences

have   distributions similar to those shown in Fig. 4, and the

orientation bandwidths have a distribution similar to that in Fig. 3 .

More globally the distributions of orientation preferences and center

frequencies change with retinal eccentricity. An important question

is the degree to which orientation tuning and spatial frequency

selectivity are interrelated. These two aspects appear to be

functionally separable since orientation tuning bandwidth for

supragranular neurons (Mansfield et al, 1980) or presumed supra-

granular neurons (Schiller et al, 1976b) does not appear to change

with retinal eccentricity at least up to 20 degrees. On the other

hand since receptive field size and center frequency are correlated;

and bandwidth is roughly proportional to center frequency (1-2 octaves);

and center frequency shifts with retinal eccentricity (Schiller et

al, 1976c) there is a change in absolute bandwidth with retinal

eccentricity. A deeper question is how the population response

profile information is utilized for a particular task.

iii) Detection mechanisms

        The ensemble of supragranular pyramidal neurons forms an

input array to the rest of the visual system that carries the necessary

and sufficient information for optimal acuity performance. If $I(x,y)$

denotes the luminance distribution in the retinal image, then the neural

response of a particular class of orientation selective neurons at the

corresponding retinotopic point, $N_{\theta,f}(x,y)$ is given by the equation

$$N_{\theta,f}(x,y) = S[I(x,y)] \qquad (5.4)$$

where S is the visual system operator. The operator can be con-
sidered to be linear if the input to the neurons is exclusively
from X cells since by definition they respond linearly. The
luminance distribution can be written in terms of the Dirac
delta function, $\delta(x - \xi, y - \eta)$, as follows

$$I(x,y) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} I(\xi,\eta)\delta(x - \xi, y - \eta)d\xi d\eta \qquad (5.5)$$

Then substituting this definition of $I(x,y)$ in Equation 5.4 and
using the linearity of the S operator since the input to the
supragranular layers is dominated by X-cell input, we obtain

$$N_{\theta,f}(x,y) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} I(\xi,\eta)S[\delta(x - \xi, y - \eta)]d\xi d\eta \qquad (5.6)$$

But the operation of S on the delta functions is simply to produce
spatial filter functions $h(x,y;\xi,\eta,\theta)$ which correspond to the
excitatory profiles previously discussed so that

$$N_{\theta,f}(x,y) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} I(\xi,\eta)h(x - \xi, y - \eta, \xi, \eta, \theta)d\xi d\eta \qquad (5.7)$$

That is to say the response of the neurons, the integrated discharge,
is the convolution of the luminance distribution with the excitatory
profile of the receptive field. Such detailed considerations
based upon the present limited knowledge of synaptic circuitry in
the central visual system cannot be extended with confidence beyond
the striate cortex. How then can visual behavior be dealt with in
a predictive quantitative manner: by choosing a visual task that
requires optimal performance such as visual acuity and by considering
what an optimal information processing system can do given the

output array from Vl. As will be seen optimal or near optimal

detection can be carried out by at least two neurally realizable

mechanisms shown schematically in Fig. 7.

Insert Fig. 7 about here

In discussing the detection process involved in visual acuity

we need to consider the issues of the independence of noise in

different neural channels, the coherence or incoherence of the

detection and the nature of the optimal detection mechanism. An

important theorem of stochastic processes (Cinlar, 1972) states that

the sum of point processes that are Poisson is itself Poisson. For

this reason, the simplest random process, a Poisson process is

a good first approximation to the stochastic nature of impulse

trains for cortical neurons when suitably corrected for refractoriness

which is intrinsic to neural activity (Teich and McGill, 1976; Teich,

Matin and Cantor, 1978). On the other hand, the very multiplicity of

sources guarantees the statistical independence of the noise in

different channels, i.e. the noise is uncorrelated. On the issue of

coherence of the detection process, the question is whether phase

information between channels tuned to the same spatial frequency but

at different retinotopic locations is preserved. With a coherent

detector spatial frequency bandwidth and spatial summation area are

inversely related but with an incoherent detector the two are independent

The studies of receptive fields in the more rostral portions of the

visual system indicate that the fields are large but in general do

not show correspondingly specific spatial frequency tuning so incoherent

detection is the most likely form. In order to detect a pattern of

interest presented to the retina the central mechanisms can be considered

to monitor the output of M orthogonal channels and perform a decision

process that is independent of spatial phase except locally. Optimal

detection arises from the application of the Neyman-Pearson criterion
which maximizes the probability of detection with the probability
of a false alarm constrained to a particular value as described by
the theory of signal detectability (Peterson, Birdsall and Fox,
1954; Green and Swets, 1966).   The general decision
rule can be stated in terms of likelihood ratios but for a Poisson
noise-counting distribution the decision rule reduces to a simple
comparison of a pulse count to a criterion number of pulses, a
threshold process readily realizable in terms of known neural mechanisms.
In the case of small signals, the optimal detector is closely approx-
imated by a multi-band detector, i.e. one that simply compares the
sum of the outputs of the M channels to a criterion level (Cohn, 1978).
Moreover, the optimal detector is also closely approximated by
another suboptimal detector, one in which detection occurs if the
activity in at least one channel exceeds a threshold (Nolte and
Jaarsma, 1967; Green and Weber, 1980). Such a probability summation
detector is readily realizable as a neural OR-gate and is computationally
particularly convenient. The detection process in a visual acuity
task then can be conceptualized in terms of a set of orthogonal spatial
filters with uncorrelated Poisson noise followed by an incoherent but
quasi-optimal detector.

IV. Behavioral Experiments

Behavioral performance reflects organized cellular, mainly
neural, activity and for a detailed understanding requires precise
information about the underlying neural activity. However, optimal
performance can be considered within the context of a computational
theory without complete information of all neural activity but rather

only the neural activity that sets constraints on optimality. In
the case of simple visual acuity optimal performance is constrained by
the spatial filtering carried out by the cortical receptive fields in
the supragranular layers of V1. A comparison can be made between
experimentally determined spatial visual acuity and the predictions
of a computational theory based on an optimal incoherent detector
constrained by M linear orthogonal spatial filters having characteristics
like the cortical receptive fields for a particular set of stimulus
conditions. However, there is a developing consensus that such a
computational theory can be extended to a wide class of stimuli.

A. Comparisons under stabilized viewing

The close correspondence in behavioral capacity among Old
World anthropoids makes possible the comparison of visual performance
in man with predictions from a computational theory based upon neural
parameters derived mainly from the macaque monkey. Visual acuity
assessed by contrast sensitivity functions is essentially identical in
man and macaque monkey when measured under the same stimulus conditions
(DeValois, Morgan, and Snodderly, 1974). For oriented grating targets
the cross-species similarity assumption for neural mechanisms is quite
plausible but the experimental conditions under which the neural data
were collected must be carefully considered.

Precise assessment of single unit receptive fields necessitated the
control of eye movements typically by immobilizing the ocular and skel-
etal musculature with a curare-like drug, gallamine triethiodide (Schil-
ler et al, 1976a; Mansfield et al, 1980). Even with drug-induced
paralysis of the neuromuscular synaptic transmission there is some
residual eye movement but it is on the order of only 0.1° over the

course of 10 minutes. Similar drug-induced paralysis in human

observers results in a reduction in apparent contrast so that large

uniformly illuminated objects disappear and edges fade (Stevens,

Emerson, Gerstein, Kallos, Neufeld, Nichols and Rosenquist, 1976),

a phenomenon observed in normal vision for peripheral targets viewed

with steady eccentric fixation under dim illumination. Such Troxler

fading is confined to the periphery since the small eye movements

present in steady fixation are small relative to the dimensions of

the receptive fields engaged by the stimulus. Steady fixation with

foveal viewing does not achieve the same result since even in the best

normal observers the direction of gaze about a fixated target is

erratic having a mean radius of about 0.1° and microsaccades are not

suppressed (Higgins, Daugman, and Mansfield, 1980). In order to ex-

amine visual performance under comparable conditions to the neuro-

physiological experiments in "any detailed psychophysical task would

have required hours of total paralysis - a very unrealistic require-

ment" (Stevens et al, 1976). An alternate means of achieving retinal

image stabilization is to compensate optically for image motion on the

surface of the retina.

The conventional approach developed twenty five years ago involves

the use of a contact lens either with a mirror attached to form one

arm of an optical lever (Riggs, Ratliff, Cornsweet and Cornsweet, 1953)

or to carry a miniature projector (Ditchburn and Pritchard, 1956).

These methods, however, are limited both in the range of stimuli that

can be presented and in the ease with which extended and detailed ob-

servations can be made in several observers because of the specially

fitted scheral contact lenses involved. Recent innovations in the

methods of accurate eyetracking which do not require physical contact

have set the stage for a new technique of retinal image stabilization.

The approach uses infrared light reflected from the eye to determine eye position. As shown schematically in Fig. 8 the novel feature is that the

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Insert Fig. 8 about here

SRI Dual Purkinje Image Eyetracker monitors infrared reflections from both the cornea (1st Purkinje image) and the back of the lens (4th Purkinje image) (Cornsweet and Crane, 1973; Clark, 1975). By measuring the optical distance between the two images, the eyetracker achieves an accuracy of greater than 1' of arc. Such a high degree of accuracy suggested to B. R. Wooten of Brown University the possibility of developing a means of retinal image stabilization without contact lenses. In the Wooten modification a pair of fast response (1-2 msec risetime) galvanometer driven mirrors use the horizontal and vertical eye movement signals of the eyetracker to compensate optically for movement of the stimulus across the retina resulting from eye movements.

Figure 9 shows an observer in the apparatus and a typical stimulus pattern

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Insert Fig. 9 about here

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on the display oscilloscope. The observer views the target monocularly and holds his head steady by means of a hard wax bite bar. Typically mydriatic and cycloplegic drugs are used to maintain the pupil at maximal dilation and the lens in a relaxed state of accommodation. A television-like raster scan on the face of the display oscilloscope can be readily produced by waveform generators to yield a uniformly illuminated surface. The voltage on the Z-axis of the oscilloscope can be modulated in phase with each frame of the scan to produce patterns on the display face using electronic hardward for simple sinusoidal patterns or digital to analog read-out from a computer for more complex patterns

The choice of a target stimulus with which to probe the visual system and test the range of validity of the computational theory

outlined above depends upon several characteristics of the primate

visual system. By using low contrast patterns the response remains

in the linear range. By choosing patterns with a small spatial ex-

tent a piece-wise isoplanatic approximation can be made to retinal

inhomogeneity. A sinusoidally-modulated luminance grating such as

that shown in Fig. 9B is easily generated and controlled and can

be used to determine the frequency response which is related to

the line-spread function by a Fourier transform. The case of foveal

vision is of particular interest and Fig. 10 shows three results

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Insert Fig. 10 about here

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obtained for a small grating patch centered at the fovea ($\pm$ 1°)

surrounded by a broad border of approximately equal luminance to

eliminate edge effects which could swamp the response of interest.

Temporal transients also are avoided by the use of a relatively long

display period.

The basic datum consists of an observer's contrast threshold

setting but each data point is typically based on several observations

to obtain an accurate average. Fig. 10A displays detection threshold

as a function of target orientation for a grating of relatively high

spatial frequency. The solid line drawn through the data points is the

prediction from the computational theory scaled to the sensitivity

level of the observer. The results show how the orientation anisotropy

present in the neuronal population translates into a difference in the

detectability of targets at different orientations. These results

are generalized in Fig. 10B which shows detection threshold as a

function of spatial frequency of the grating target for both a vertical

and an oblique angle (45°). The solid line is again the theoretical

prediction from computation. 'At low spatial frequencies the sensitivity

is depressed beyond that inherent in the frequency response of the

central fovea because the limited number of grating cycles present

in the small 2° target decreases the optimization of detection pro-

duced by the information pooling that can take place when multiple

bars are present. However, the convergence of the vertical and

oblique sensitivities reflects the dominance of the response by

the Y cells which do not exhibit orientation anisotropy. The

effect on detection threshold of prior exposure to a high contrast

grating target is shown in Fig. 10C. The solid line represents the

theoretical curve generated from the computational theory by taking

the difference in the pooled neural response before and after

adaptation. The selective elevation of threshold reflects the

orientation selective nature of the pattern adaptation. Since

the pooling operation in effect averages over the spectrum of

orientation tuning curves the resulting curve resembles the tuning

curve of the average receptive field.

B. Implications for pattern detection

There is accumulating evidence that the detection of a

wide class of monochromatic patterned stimuli can be explained by

a computational theory based on quasi-optimal incoherent detection

applied to the output of an array of independent channels whose

medium bandwidth filter characteristics resemble the receptive

field excitatory profiles of efferent neurons in the supragranular

layers of V1. Incoherent detection is consistent with the localized

effects of pattern adaptation. Previous work from this laboratory

(Legge, 1976) demonstrated that the adaptation is retinotopically

localized. Legge found that adaptation to a high contrast fine line

did not affect subsequent detection of spatially extended sinusoidally

modulated grating patterns as would be predicted if the effect of

adaptation were local rather than global. Daugman and Mansfield (1979)

found that the adaptation is not even transferred interhemispher-

ically since no adaptation is produced by an eccentric high contrast

grating patch placed in the homologous location in the opposite

hemifield. Graham and her colleagues (Graham and Nachmias, 1971;

Graham, Robson and Nachmias, 1978) have demonstrated independence

of detection of separate components in a compound grating even

when presented to a relatively homogeneous retinal region, a result

consistent with the existence of independent channels. Variation

with retinal eccentricity of several measures such as visual acuity

(Aulhorn and Harms, 1972), summation area (Westheimer, 1967), Mach

band locations (Shipley and Wier, 1972), contrast sensitivity functions

(Hilz and Cavonius, 1974), and line spread functions (Hines, 1976;

Limb and Rubinstein, 1977; Wilson, 1978) are consistent with an increase

in receptive field size with distance from the fixation point. The

work from Wilson's laboratory in particular suggests that the increase

is linear at least up to 4°. The scatter in receptive field sizes

and types at a given retinotopic projection point is reflected in the

differences in detectability of different patterns presented at the

same retinal locus (Kulikowski and King-Smith, 1973; Wilson and Geise,

1977). Experiments with frequency gradient patterns (Wilson and

Geise, 1977) and with artificial central scotomas (Kelly, 1978) indicate

that all receptive field sizes are represented in the foveal projection

region but that there is a decline in the relative proportion of small

receptive fields with retinal eccentricity. On the important issue

of the estimate of the spatial frequency bandwidth of the receptive

fields a growing consensus indicates that although several studies have

been interpreted as implying extremely narrow bandwidths (1/4 octave)

(Sachs, Nachmias and Robson, 1971; Kulikowski and King-Smith, 1973;
Quick and Riechert, 1975) subsequent work has shown that if an inco-
herent detection process such as probability summation across space
is taken into account the data are consistent with medium bandwidths
(Mostafavi and Sakrison, 1976; Stromeyer and Klein, 1975; Graham
and Rogowitz, 1976; King-Smith and Kulikowski, 1975; Wilson, 1978;
Wilson and Bergen, 1979; Bergen, Wilson and Cowan, 1979). The band-
width estimates range from 1.5 to 2.1 octaves at half-height. The
data of Blakemore and Campbell (1969) obtained using spatially sel-
ective frequency adaptation yields an estimate of 1.5 octaves full
bandwidth at half-height but retinal inhomogeneity and probability
summation are not taken into account resulting in an underestimation.
Mostafavi and Sakrison (1976) obtained an estimate of 2.1 octaves using
band-limited noise displays taking into account retinal inhomogeneity
and spatial probability summation but not summation over channels
resulting in an overestimation. Wilson and his colleagues (Wilson,
1978; Wilson and Bergen, 1979; Bergen, Wilson, and Cowan, 1979) us-
ing subthreshold summation to determine the line-spread function
found 1.75 octaves taking into account spatial probability summation
over channels and space. The monkey neurophysiology data as described
earlier yields estimates of 1 - 2 octaves (Schiller et al, 1976c;
Poggio et al, 1977; DeValois et al, 1978). De Valois et al's measure-
ments made under conditions comparable to the psychophysical measure-
ments gave a median value of 1.4 octaves and 1.2 octaves for the
more orientation selective neurons. A similar situation holds for
orientation selectivity. Early studies particularly those that em-
ployed subthreshold summation, e.g. Kulikowski, Abadi and King-Smith
(1973) were interpreted as evidence for extremely narrow orientation
bandwidths. e.g. ± 3°. Other measurement procedures using adaptation

(Blakemore and Nachmias, 1971) and masking (Campbell and Kulikowski, 1966) gave estimates of $\pm 7^{\circ}$ to $\pm 15^{\circ}$. However, these studies did not take into account spatial probability summation. By taking spatial probability summation into account the data from subthreshold summation experiments are consistent with orientation bandwidths on the order of $\pm 16^{\circ}$. Mostafavi and Sakrison (1976) using two dimensional filtered noise and assuming a Gaussian shape, retinal inhomogeneity and a spatial probability summation index of 6 obtained an orientation bandwidth of $\pm 14.4^{\circ}$; however, they did not take into account summation across channels or orientation anisotropy. As we have seen taking into account spatial probability summation, orientation anisotropy and probability summation across channels yields an estimate of $\pm 20^{\circ}$ (see Fig. 10C). The neurophysiological data uniformly concur on an estimate of average bandwidth of $\pm 20^{0}$ to $\pm 25^{\circ}$ (Schiller et al, 1976b; Poggio et al, 1977; DeValois et al, 1978; Mansfield et al, 1980). The concordance of results from behavioral and neurophysiological studies particularly regarding orientation and frequency bandwidths carries a number of implications for visual processing. For example, the view that the visual system performs some type of Fourier analysis on a visual scene (Campbell and Robson, 1968; Blakemore and Campbell, 1969; Pollen, Lee and Taylor, 1971) is oversimplified at best since the channel bandwidths are too broad. The apparent sharp tuning is the result of the statistical nature of the incoherent detection process. On the other hand an alternative view consistent with experimental facts reviewed here is that the visual system analyzes target objects using an ensemble of medium bandwidth spatial filters whose characteristics match those of the receptive fields of supragranular striate cortical neurons.

V. Future Prospects

The development of a truly computational theory of primate
vision is an exciting prospect but one that can be realistically
approached. Two guiding principles have emerged from the studies
reviewed here. First the primate visual system is organized in
terms of functionally significant channels. Secondly optimal visual
performance can be analyzed into a critical transformation site
and optimal utilization of the information from that site. The
filtering operations performed by the visual system up to the level
of the striate cortex and by the striate cortex itself give rise
to a filtered neural image of the retinal stimulus represented by
the population response profile of the efferent neurons, the trans-
cortical projection of which consists of the pyramidal cells in
the supragranular layers. This neural image contains all the fine
grain information available to the more rostral portions of the
visual system which operate upon the information in a manner similar
to a noncoherent optimal detector. In the detailed example the
stimuli were stationary, low contrast, monochromatic, monocularly
presented targets and the task was one of detection. Each of these
restrictions can be lifted or modified.

The neurons in the supragranular layers respond differentially
to direction of target motion, but no quantitative comparison has
been made with the directionally sensitive mechanisms revealed by
prior adaptation in psychophysical experiments. One experimental
finding which makes reasonable the suggestion that these neurons
mediate the detection of target direction is that target detection
is superior to detection of direction of motion even in the absence
of eye movements achieved using retinal image stabilization

(Mansfield and Nachmias, 1980), a result consistent with the dominance of X-input over Y-input into these layers. Although the simplest cases to analyze are those at threshold, linearity extends about that level (Mansfield, 1976a). Indeed as Cannon (1979) has shown the entire contrast sensitivity curve remains parallel to those generated from equal apparent contrast up to at least a 70% contrast ratio. At suprathreshold levels in the linear range, the spatial filtering imposed by the striate cortex has predictable but not intuitively obvious consequences such as the distortions from veridicality epitomized by the familiar optical illusions (Ginsburg, 1979) or, for instance, the spatial distribution of eye saccades and fixations in free viewing of even a complex target such as a face (Ginsburg, Mansfield and Higgins, 1980). Saccadic eye movements also induce an adaptive suppression of retinal blur by masking that is spatially frequency tuned and can be modelled in terms of inhibitory interactions between fast and slow responding spatial filters (Breitmeyer and Ganz, 1976; Rogowitz, 1980). Within the same conceptual framework, binocular interactions such as interocular adaptation and masking or even local stereopsis can be usefully analyzed in terms of striate neuronal activity. On the other hand, successful extension of the approach of the cellular synthesis of behavior described here to more complex visual perceptual and visuomotor behaviors such as global stereopsis, object color determination and object tracking will require a more detailed understanding of the primate visual system particularly of regions beyond V1.

The basis for a new and detailed understanding of the primate extrastriate cortex will rest on three developments in cellular and behavioral neurobiology. First, information on

the general functional subdivision of labor among the different regions. A recurrent theme of the chapters in this volume is the existence of visual subsystems, and a premier goal of behavior analysis must be that of fractionating an animal's repertoire into units that optimally engage a particular subsystem. Insights into causal sequences in the dynamic unfolding of a behavioral script are now possible with single and multi-unit recording from alert animals in well defined behavioral tasks with eye movements closely monitored (e.g. the study by Lynch, Mountcastle, Talbot and Yin (1977) of the initiation and control of visual grasping of an object of motivational significance). On the other hand, anatomical labelling of a subsystem by its elevated metabolic activity when engaged can be accomplished by using ^{3}H- or ^{14}C-2 deoxyglucose which accumulates in cells since it does not substitute for glucose beyond a certain point in the Krebs cycle (for example, Frost (this volume) using this technique has localized the region of a pigeon's brain dealing with relative motion).
In the living animal positron emission transverse tomography will soon both supplement the resolution of metabolic activity on the cortical surface now possible with gamma emission and provide resolution in three dimensions eventually down to the millimeter level. Secondly, an extensive knowledge of the interconnections between cortical regions and the interactions with subcortical structures. Area Vl is the simplest visual cortical area in terms of its connections and yet it is reciprocally interconnected with at least four other structures: dLGN, the pulvinar complex, and Areas Vl and MT. Although

connections can sometimes be inferred from disconnection
syndromes produced by lesions, such an approach, applied to a
distributed processing system such as the visual system,
particularly in advance of anatomical investigations, can
frequently yield paradoxical results (see chapters by Dean
and by Levine for a discussion of such inferences for infero-
temporal lesions). Fortunately, recent advances in neuroanatomical
labelling by axonal transport have brought this question within
the range of experimental analysis so that precise information is
accumulating (see Van Essen (1979) for an excellent recent
review). Since the function played by a particular region is
determined not only by the intrinsic operations it performs
but by the pattern of its afferents and efferents in the
circuit of which it forms a part, even a first approximation
to the necessary circuit diagram such as the one illustrated
in Fig. 1A provides a rational basis for identifying functional
subsystems (see the chapter by Ungerleider and Mishkin discussing
two cortical visual subsystems: one terminated by the infero-
temporal region TE and the second by the inferior parietal
lobule, area PG). Thirdly, an understanding at the synaptic
level of the functioning of cortical columns, the modules of
organization of the neocortex. Although a connectional
diagram even as detailed as Fig. 1B together with recording and
lesion studies can illuminate the role of a particular region,
for example that of the striate cortex as a preprocessor of object
information but the mechanimsm by which the cortex operates
upon its afferent input requires a more fine grain analysis.
As Mountcastle (1976) points out: "the central problem of the

intrinsic physiology of the cerebral cortex is to discover

the nature of the neuronal processing within the translaminar

chains of interconnected cells (in columns)." Techniques are

now available to determine the synaptic circuitry of morpho-

logically identified neurons in functional modules of neocortex

using in vitro recording from brain slices (Mansfield and

Simmons, 1979; Mansfield, in preparation). Anatomical and

physiological evidence (see review by Mountcastle, 1978)

suggests that cortical modules may have a unitary organization

so that detailed knowledge of the synaptic organization in one

cortical region could serve as a paradigm for the cortex as

a whole. The present and continuing challenge will be to

synthesize the results from these three lines of development

into a coherent computational theory of visual behavior.

Acknowledgements

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Figure Captions

Figure 1.   Anatomical organization of the primate visual system.
Nomenclature: R is the retina; X, Y, W designate the axons
of three classes of ganglion cells or at the geniculate the
projections to and from the parvocellular and magnocellular
layers, see Fig. 1B; DLGN is the dorsal lateral geniculate
nucleus; PT is the pretectum; SC is the superior colliculus;
PL is the lateral pulvinar; PI is the inferior pulvinar;
V1 is the striate cortex; V2 etc. are the prestriate visual
areas (See Van Essen, 1979); IT is the inferotemporal cortex
(cytoarchitectonic areas TEO and TE of von Bonin and Bailey);
FEF are the frontal eye fields in the region of the arcuate
sulcus consisting of cytoarchitectonic areas 8A, 8B and
posterior 9 in the terminology of Brodmann; MT is a region
at the posterior end of the temporal sulcus described as
the visual area of the superior temporal sulcus by Zeki (1971)
but probably homologous to the middle temporal area in the
owl monkey; IPS(OA) is a region delineated by Ungerleider
and Mishkin (this volume) using anterograde transport from
V1 of radioactive amino acids in area OA (von Bonin and Bailey)
at the depth of the posterior extent of the intraparietal
sulcus; IPS(PG) is a region delineated by Mesulam, van Hoesen,
Pandya and Geschwind (1977) using retrograde transport of
horseradish peroxidase from PG and is located in the
intraparietal sulcus anterior to IPS(OA); TF is a region
described by von Bonin and Bailey on the medial surface of

the temporal lobe adjacent to TE and OA; IPL(PG) is the
region PG described by von Bonin and Bailey on the inferior
parietal lobule and corresponds approximately to the posterior
half of area 7 of Brodmann.

A. Schematic representation of the main structures showing
    the principal pathways with arrows indicating the direction
    of flow of information and control. For clarity of
    presentation only ipsilateral connections have been shown
    and the detailed structure of the limbic and motor systems
    and that of the prestriate visual cortical field has been
    omitted. For purposes of this diagram area 6aβ, premotor
    cortex, which receives a projection from area 9p in FEF
    is included in the motor system along with the pons
    (which receives input from IPL(PG), MT and intervening
    regions (Glickstein, Cohen, Dixon, Gibson, Holland,
    Labossie and Farrel, 1980)) and the interstitial nucleus
    of Cajal (which receives input from the superior colliculus).
    Major sources of evidence for the newly described pro-
    jections in the cortical visual field: projections to
    IPL(PG) are based on Mesulam et al. (1977) and Divac,
    LaVail, Rakic and Winston (1977); projections to and from
    limbic system based on Nauta and Domesick (1980); pro-
    jection from motor system to visual cortical field based
    on Johnston, McKinney and Coyle (1979); projections from
    FEF (areas 8 and 9p) based on Kunzle and Akert (1977)
    and Kunzle (1978); projection to IPS(OA) based on
    Ungerleider and Mishkin (this volume); connections to
    and from V1 based on Lund et al. (1975). The dashed

rectangles indicate structures whose substructures are
not indicated or not known in detail, e.g. prestriate
visual areas. Arrows to dashed rectangles indicate
projections to more than one substructure; arrows from
such rectangles indicate projections from more than one
substructure.

B. Schematic representation of the main structures
in the retino-cortical pathways with arrows indicating
the direction of information flow. For clarity of
presentation only the connections from one hemi-retina
and to one hemisphere are shown. The brackets on the
left-hand side of the lateral geniculate nucleus indicate
feedback distributed over the parvocellular (upper bracket)
or magnocellular (lower bracket) layers. Major sources
of evidence: for the existence and distribution of
X, Y and W type retinal ganglion cells (DeMonasterio,
1978a, 1978b; Schiller and Malpeli, 1977); for the pro-
jections from retina to superior colliculus and pretectum
(Schiller and Malpeli, 1977; Bunt, Hendrickson, Lund,
Lund and Fuchs, 1975); for the connections from retina to
dorsal lateral geniculate nucleus (Dreher, Fukada and
Rodieck, 1976; Schiller and Malpeli, 1978); for the pro-
jections from geniculate to striate cortex (Hubel and
Wiesel, 1972; Rezak and Benevento, 1979); for the pro-
jections from striate cortex to cortical and subcortical
structures (Lund et al., 1975; Van Essen, 1979; Maunsell,
Bixby and Van Essen, 1979; Ogren and Hendrickson, 1976;
Rezak and Benevento, 1979); for feedback connections to

striate cortex (Van Essen, 1979; Ogren and Hendrickson, 1977; Wong-Riley, 1979); for connections among superior colliculus, pretectum and their projections (Benevento and Fallon, 1975; Rezak and Benevento, 1977; Berman, 1977 (cat); Benevento, 1980); for feedback from V2 and MT to geniculate (Lin and Kaas, 1977 (owl monkey)).

C. Schematic diagram of anatomically segregated visual processing in striate cortex (after Mansfield, 1979).

Figure 2. Orientation selectivity in binocular bidirectional

striate neuron in monkey. (After Mansfield et al., 1980)

A. Anatomical reconstruction of microelectrode

track. On the left side of the diagram the

nomenclature for each distinguishable lamina

of the striate cortex is indicated. The

solid black circles represent the locations

of 4 marking electrolytic lesions. The short

line segments perpendicular to the solid line

marking the track represent the recording sites

of isolated single units. The solid black arrow

indicates the recording site of Unit 8T107

described more fully in Figures 2B and 2C.

B. Receptive field map and response profile.

The solid black rectangle represents the

minimal discharge receptive field of the neuron

in the right visual hemifield. The receptive

field measured $1/2^{\circ}$ by 1° and was located

approximatley 6° from the fovea. Arranged

around the receptive field map are peristimulus

discharge histograms generated by a long slit

subtending 0.1° in width moved through the dis-

charge zone at a velocity of $5.6^{\circ}/sec$ at the

orientation indicated. Each peristimulus

histogram is based upon 15 stimulus presentations.

C. Orientation tuning curves. Integrated dis-

charge as a function of target slit orientation.

Each data point is the average calculated from

15 stimulus presentations. The solid

squares represent the responses from the

receptive field in the right eye; the open

circles represent the responses from the

receptive field in the left eye. The error

bars represent ± one standard error of the mean

integrated discharge. The solid lines fitted

to the data points represent theoretical

functions for orientation tuning derived from

a simple model of orientation determination.

(Modified from Mansfield, Ronner and Daugman (1980)).

Figure 3.   Frequency distribution of orientation selectivity

in striate neurons. Orientation selectivity was

measured as the half-bandwidth at half-maximal

response on an orientation tuning curve as shown in

the insert. The measurements were obtained from

96 independently sampled neurons. (From Mansfield

et al (1980)).

Figure 4.   Distribution of axes of orientation preference for

striate cortical neurons. Each neuron was sampled

from a single penetration with multiple penetrations

separated by at least 500 μm across the cortical

surface.

A.   Polar histogram of distribution for receptive

fields of independently sampled neurons with

foveal receptive fields. (N=82). The deviation

from uniformity is statistically significant

$(\chi^2 = 15.94,\ df = 8;\ p < 0.05)$.

B.   Polar histogram of distribution of independently

sampled neurons with parafoveal receptive

fields (N = 128). The Chi-squared test for

departure from a uniform distribution was not

significant at the 5% level (χ^2 = 1.66,

df = 8; p > 0.5).   (From Mansfield et al (1980)).

Figure 5. Frequency distribution of optimal spatial frequency

of striate cortical neurons in the foveal and

parafoveal projection regions. The curve to the

left represents the parafoveal striate neurons

from the projection region 4°-6° from the fovea.

The curve to the right represents the foveal striate

neurons from the projection region covering the

central 2°.

Figure 6. Schematic diagram of a candidate mechanism for

receptive field organization of supragranular neurons.

A.   Excitatory profile generated by retinal

lateral inhibition.

B.   Candidate neural network in supragranular

region of striate cortex exhibiting recurrent

lateral inhibition.

C.   Excitatory profile generated by operating on

profile in A. by neural network in B.

Figure 7. Schematic diagram of two quasi-optimal neurally

realizable pattern detector mechanisms.

A. Pooling detector. In this case the luminance
corresponding to the visual stimulus distribution is
processed by linear spatial filters and the responses
of the filters summed or pooled in a detector which
responds if the combined input exceeds some criterion
level. For clarity of presentation the independent
noise sources for the spatial filters have been
omitted.

B. Probability summation detector. In this case the
luminance distribution corresponding to the visual
stimulus is processed by linear spatial filters but
the response of each is handled by an independent
detector which responds if the input exceeds a criterion
level. So the action of the effector depends on the
action of one or more of the detectors. For clarity
of presentation the independent noise sources for the
spatial filters have been omitted.

Figure 8. Schematic diagram of Dual Purkinje Eyetracker and Retinal
Image Stabilization System. In determining eye position,
a low intensity invisible beam of infrared light from a
light emitting diode is reflected from the eye and the
images of the first Purkinje image (corneal reflection) and
fourth Purkinje image (posterior surface of the lens) are
separately focussed on quadrature photodetectors. The
error signals from the quadrature photodetectors drive
mirrors in the optical path via servo motors. The output
of the second quadrature photodetector (fourth Purkinje

image) then corresponds to the difference between the
first and fourth Purkinje images, a measure of eye position
that is relatively invariant under lateral movement of the
head. For retinal image stabilization the eye position
signal is used to operate galvanometer driven mirrors in
the optical path of the viewer which compensate for vertical
and horizontal eye movements by appropriate movements of
the visual target, a computer-controlled video display on
a CRT. Independent of the stabilization a set of visible
LEDs serve as fixation targets. In addition the observer's
responses are accessible to the computer and can be used
in interactive psychophysical procedures.

Figure 9.   A.   Photograph of observer viewing target under retinal
image stabilization by using the outputs of the SRI
Dual Purkinje Image Eyetracker to drive small mirrors
on the Stimulus Deflector seen in the foreground.

B.   Photograph of target on CRT at high contrast.

Figure 10.   Comparison of calculated response from synthesized striate
neuron population with human psychophysical data on
orientation acuity. The theoretical curves have been
scaled in amplitude to fit best the experimental data.

A.   Detection threshold as a function of target orientation
for a 8 cycle/degree sinusoidally modulated luminance
grating subtending 2° foveally. The circles represent
the data points; the solid line represents the computed
values.

B.   Detection threshold as a function of grating spatial
frequency. The circles represent the data points for
the vertical target; the squares represent the data

for the oblique (45°) target. The solid lines represent
the computed values.

C. Detection threshold elevation following adaptation to
8 cycle per degree grating subtending 2° foveally.
The squares represent the data obtained with adaptation
and testing in the same eye. The x's represent the
data obtained with testing in the contralateral eye.
The solid curve represents the computed values with
adaptation proportional to neural response.

PRIMATE VISUAL SYSTEM
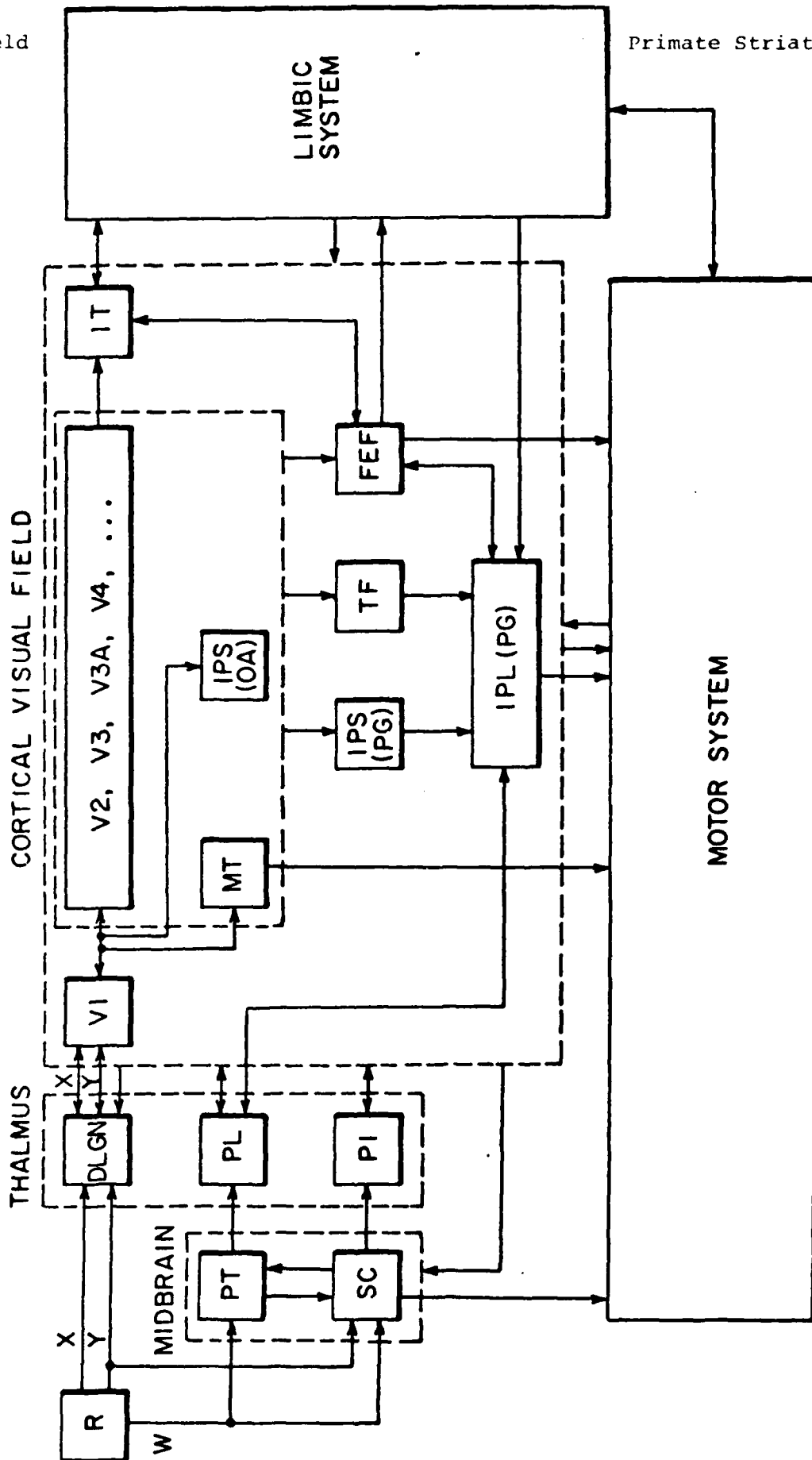
Figure 1

VISUALLY GUIDED BEHAVIOR
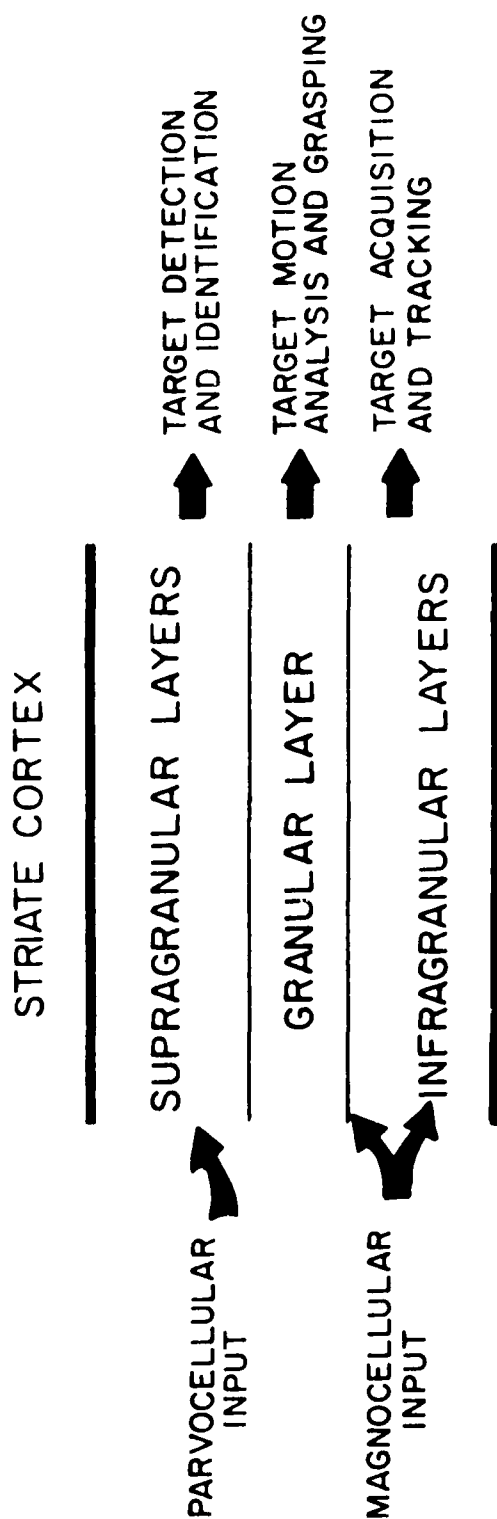
B   PRIMATE RETINO-CORTICAL PATHWAYS

Figure 1

Figure 1

A

RECONSTRUCTION OF PARASAGGITAL
OBLIQUE PENETRATION T10

LAYER

1

2
+
3

4A

4B

4Cα

4Cβ

5

6A

6B

WHITE MATTER

1 MM

L₁

L₂

L₃

L₄

Figure 2

UNIT 8T107
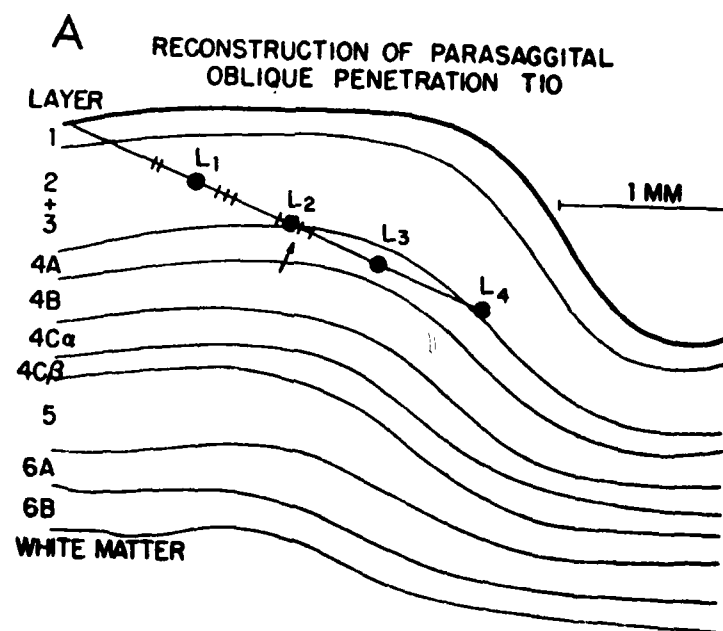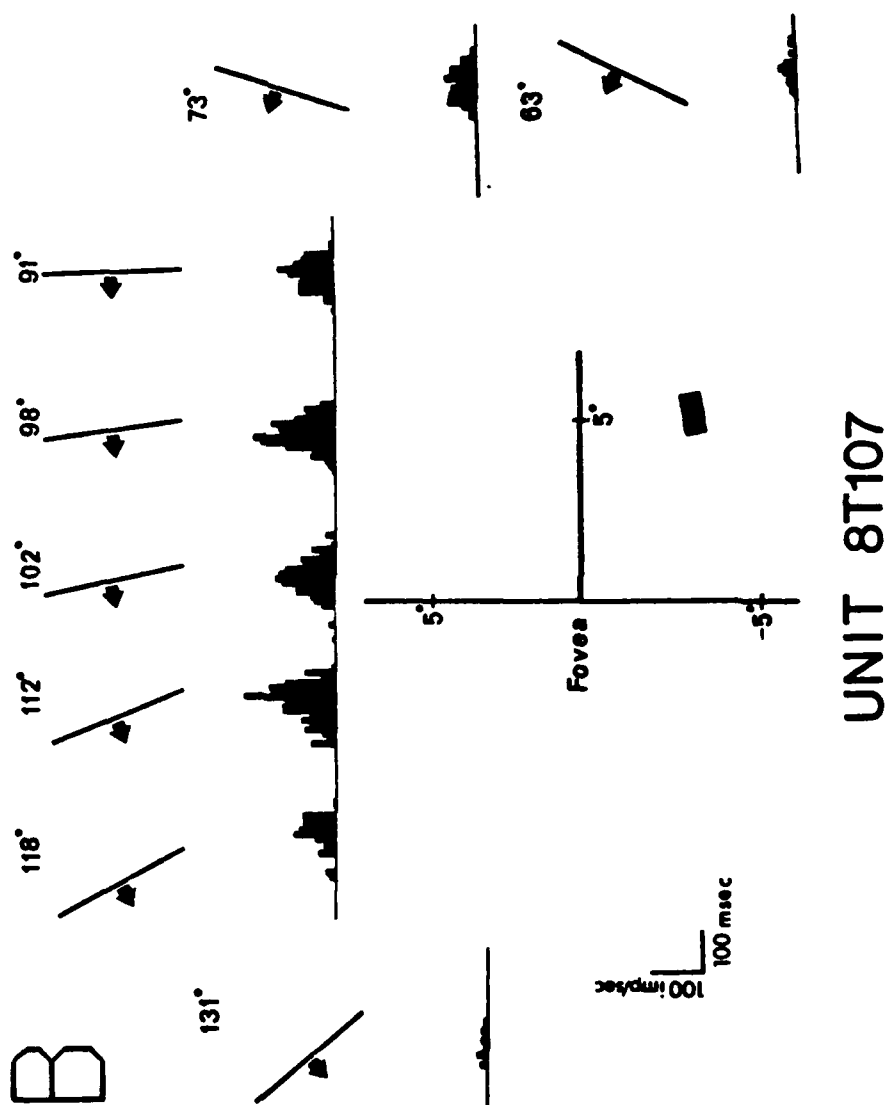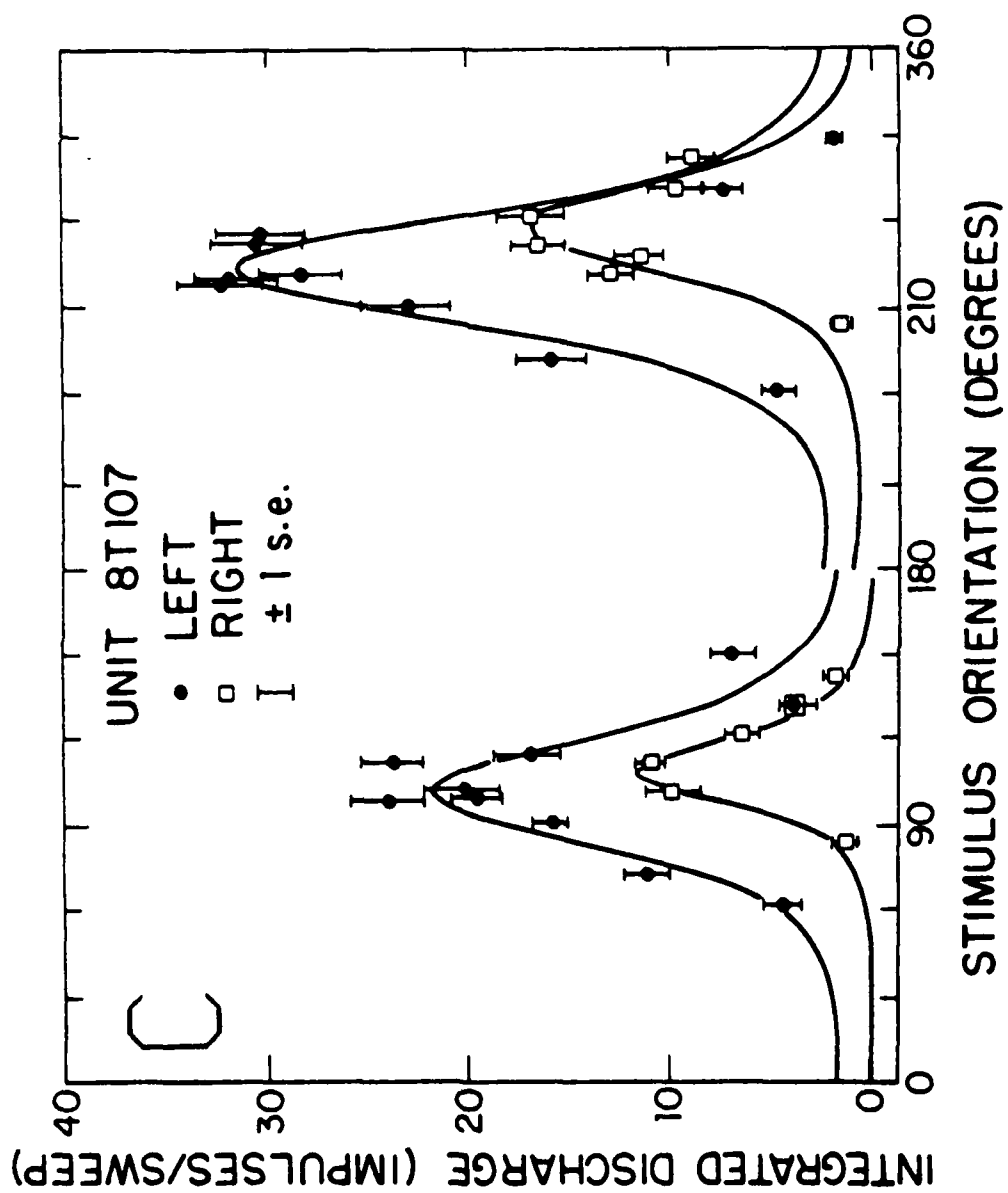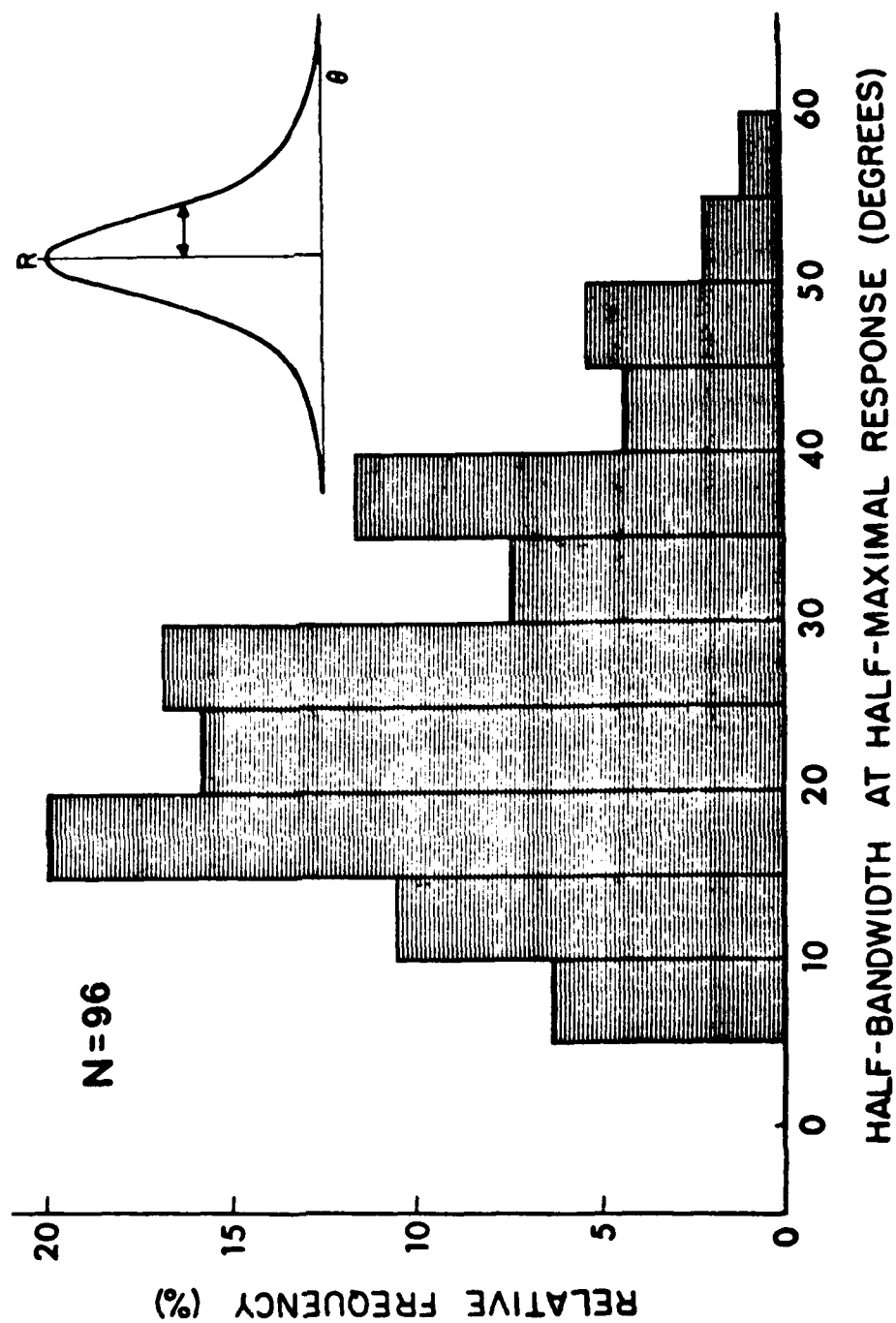
Figure 2

Figure 2

Figure 3

DISTRIBUTION OF AXIS OF ORIENTATION PREFERENCE

A

19.5%

—0°

FOVEAL
N=82

B

13.3%

—0°

PARAFOVEAL
N=128

Figure 4

DISTRIBUTION OF STRIATE NEURON OPTIMAL SPATIAL FREQUENCY
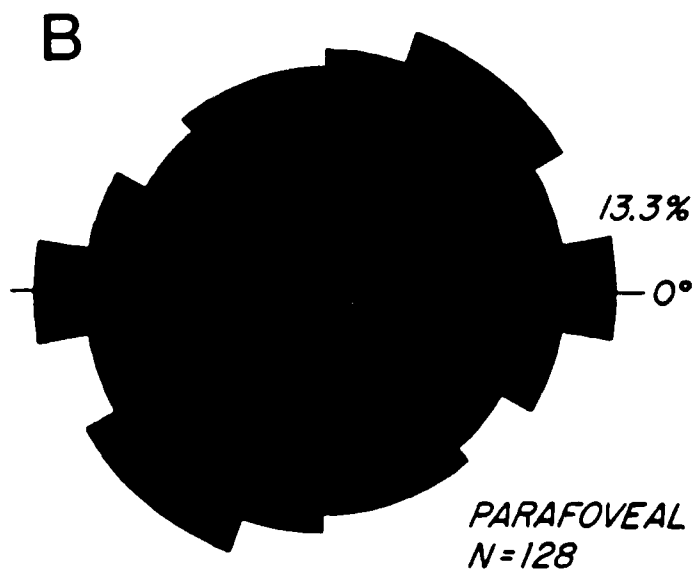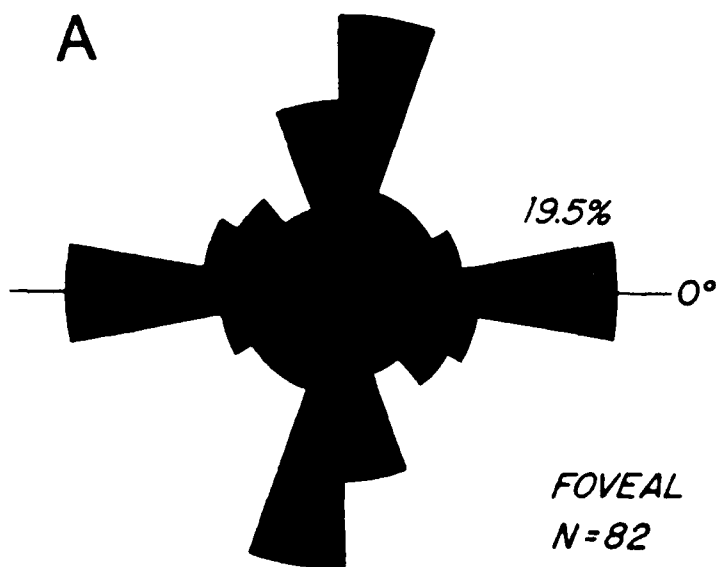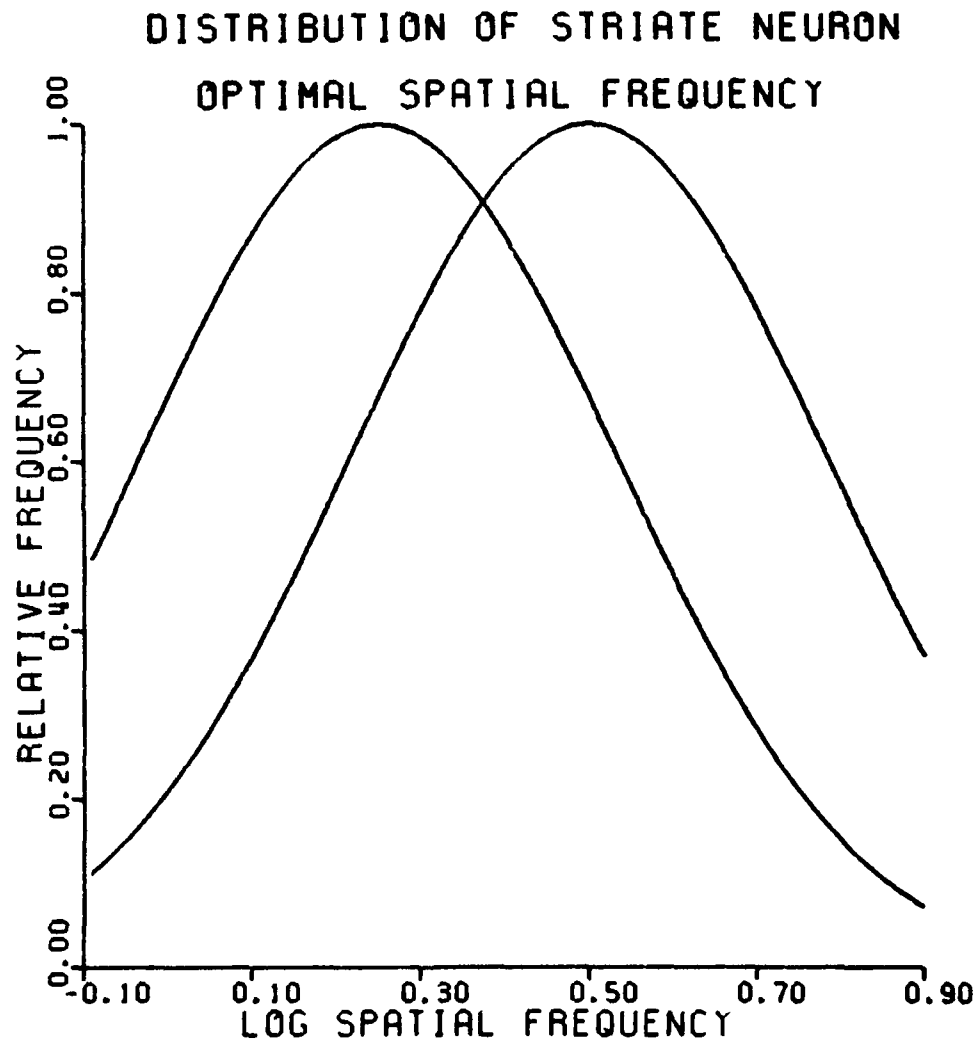
Figure 5

EXCITABILITY PROFILE

A

NEURAL CIRCUIT
FOR STRIATE CORTEX

B

EXCITABILITY PROFILE

C

Figure 6

A

POOLING

RESPONSE

EFFECTOR MECHANISM

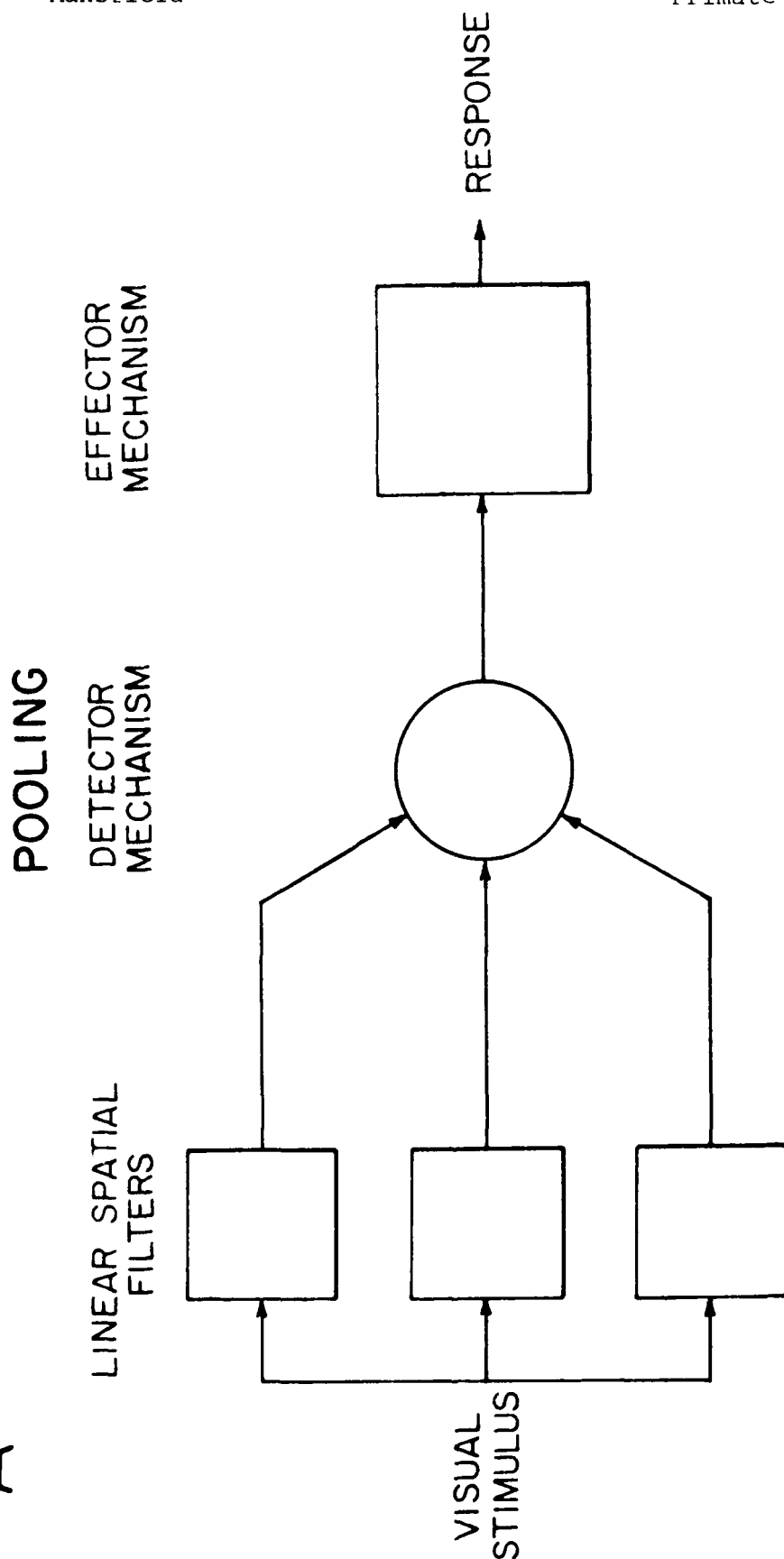DETECTOR MECHANISM

LINEAR SPATIAL FILTERS

VISUAL STIMULUS
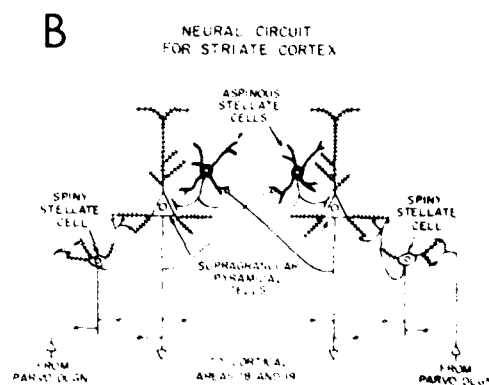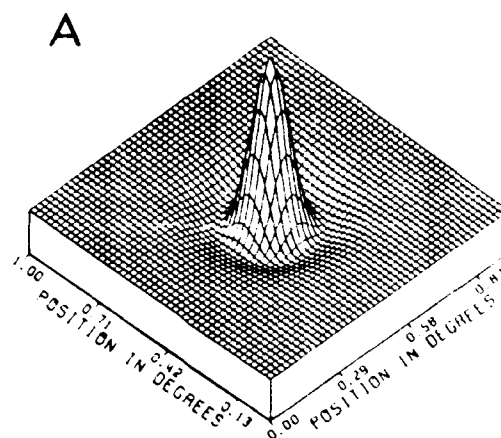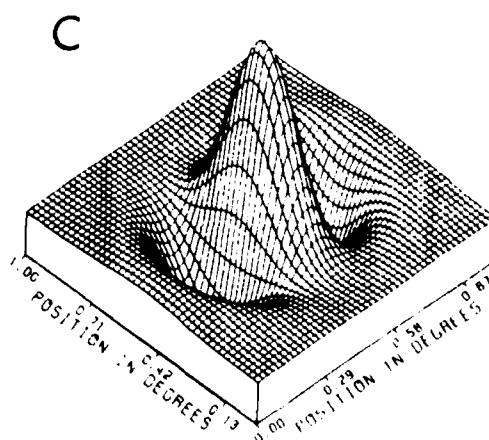
Figure 7

B

PROBABILITY SUMMATION
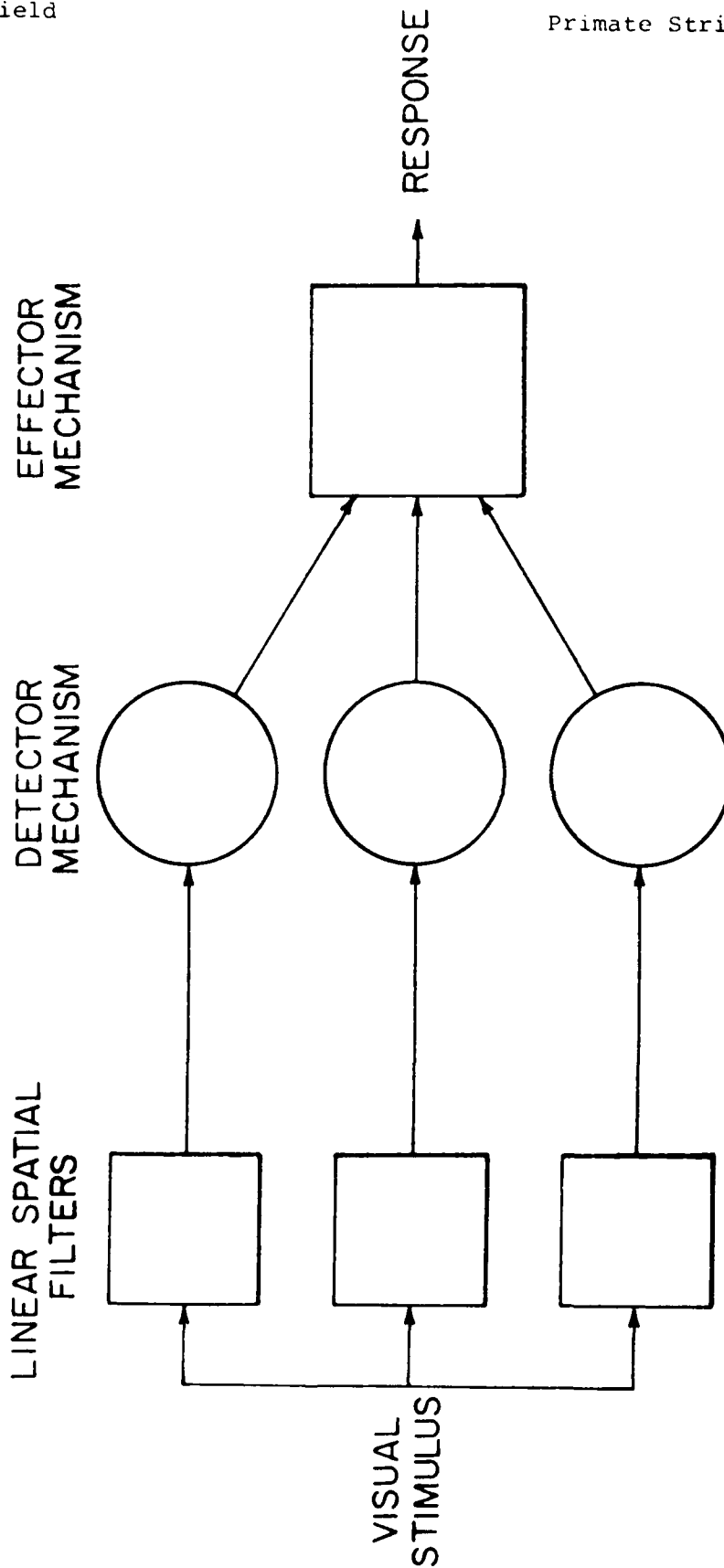
Figure 7

Figure 8

A

B

Figure 9

A

J.D.
R.M.
THEORETICAL

B FOVEAL MODULATION TRANSFER FUNCTIONS
FOR VERTICAL AND OBLIQUE GRATINGS

OBSERVER JD

VERTICAL

OBLIQUE

LOG SENSITIVITY

LOG SPATIAL FREQUENCY

C

BINOCULAR TRANSFER OF
ORIENTATION ADAPTATION

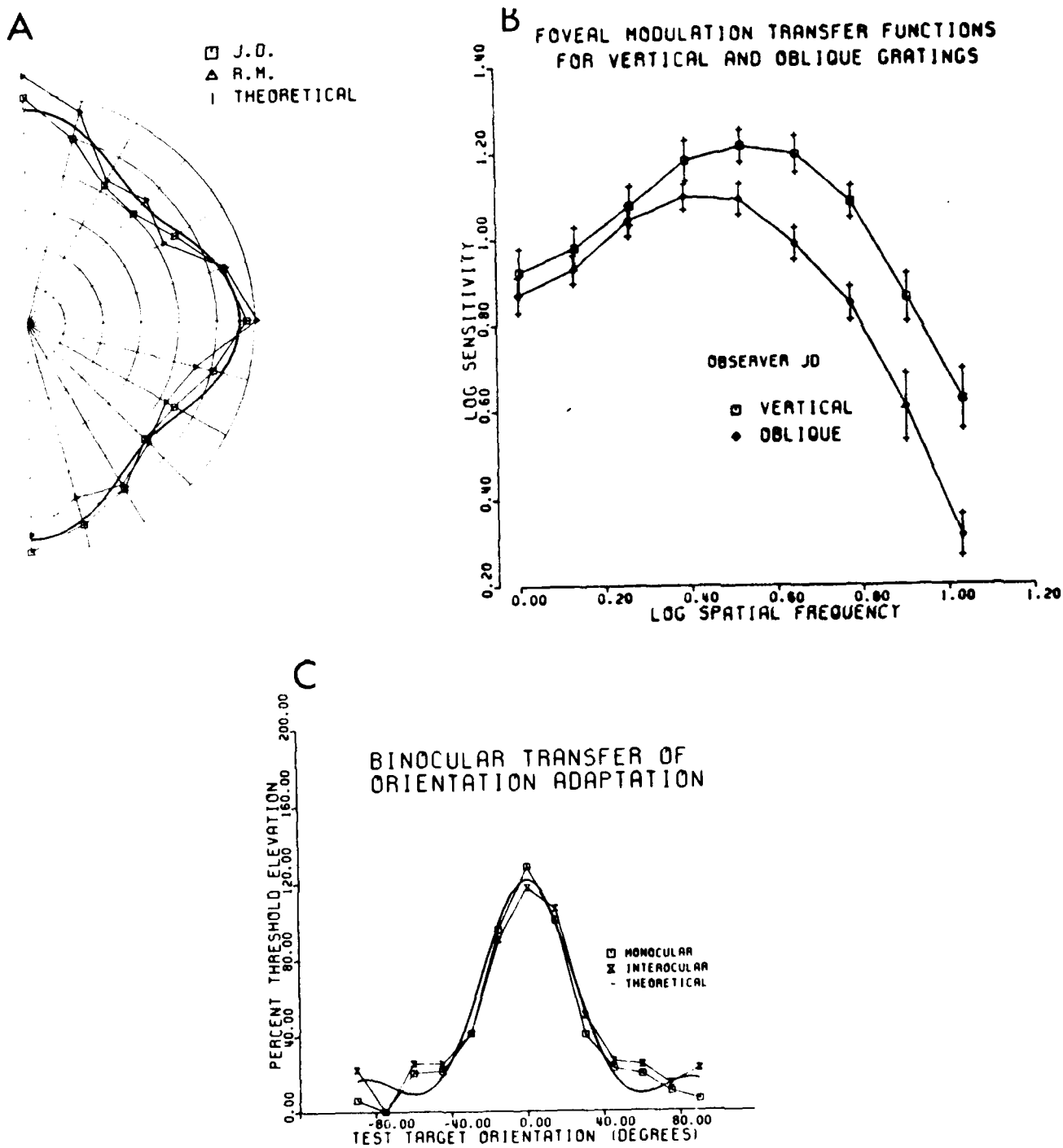PERCENT THRESHOLD ELEVATION

MONOCULAR
INTEROCULAR
THEORETICAL

TEST TARGET ORIENTATION (DEGREES)

Figure 10

DATE
FILMED

— 8